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Distribution of Progeny by *Cryptus inornatus* Pratt (Hymenoptera: Ichneumonidae)

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Introduction

In a previous paper (Ulyett, 1949), the present writer outlined a tentative classification of insects serving as hosts to entomophagous parasites. This scheme was based upon the more obvious relationships that exist between parasite and host insect and those which might conceivably have some bearing upon the degree of efficiency with which the females of the former distribute their progeny among available hosts. Five main groups were recognized which reflected the differences occurring between the various kinds of hosts and parasites encountered in the field. Of these, examples have already been dealt with from two of the groups, viz., Group II, in which the host is normally active but is paralysed by the parasite before oviposition, as exemplified by the distribution of eggs by the Braconid, *Microbracon hebetor* Say among the larvae of *Ephestia kuehniella* Zell. (Ulyett, 1945); Group IIIA, in which the host is stationary and fully exposed as illustrated by the relationship between the eggs of *Ephestia* and the attack of *Chelonus texanus* Cress. (Ulyett, 1949).

The present contribution describes the distribution of progeny by a parasite falling within a sub-division of the host/parasite category of Group II, i.e., by a parasite which attacks an active host which is in a protected situation—in this case enclosed within a cocoon. The experimental work on which this paper is based was carried out in the course of a rearing project conducted by this Bureau on behalf of the Department of Agriculture of the Union of South Africa. It formed, in fact, an essential preliminary to the large-scale programme developed, enabling the latter to be placed upon a sound basis with considerable economy in labour and material.

It has become increasingly obvious that studies such as the one about to be described are essential for the efficient conduct of parasite rearing projects, irrespective of the species of insects concerned. Apart from the immediate value of the data collected, it is clearly useful as information which is sorely needed in our general investigations in biological control. While our knowledge of the behaviour of entomophagous parasites in relation to their hosts is gradually increasing, it is still very far from being comprehensive. The individual variations exhibited by the different species so far studied show clearly that we are not yet in a position to make even the most approximate generalizations. While there are certain indications that parasitic hymenoptera may prove to fall into more or less well-defined groups, each possessing characteristics of behaviour and response to environmental factors which are common to all members of the group, it will be necessary to give attention to many more individual cases before this can become established as a working hypothesis. Nor can we attempt, at this stage, any general evaluation of the influence of the factors which serve to modify the inherent tendencies possessed by the organisms concerned. From a practical point of view, therefore, it is still necessary to treat each species individually and to test its specific reactions to the factors which are known to impinge upon it in its environment.

Cryptus inornatus Pratt has been introduced into South Africa and liberated in the Karroo region of the Cape Province against the so-called "Karoo Caterpillar", *Loxostege frustalis* Walk., which is a serious pest of the indigenous "Karoo bush" (*Pentzia* spp.—mainly *P. incana*). This "bush" is really a small, low-growing shrub which is xerophytic in character and which constitutes a most valuable fodder-plant for sheep, the rearing of which provides the main industry in this semi-arid area. The life-cycle and habits of *L. frustalis* are very similar to those of the closely-related beet webworm. The former, however, appears to be restricted to the species of *Pentzia* as food-plants and is more dependent upon climatic factors than is *L. sticticalis* (vide Taylor, 1940).

Material and Methods

Cryptus inornatus, which forms the subject of the present investigation, is a fairly large, robust species of ichneumonid which is parasitic on the larvae of the beet webworm (*Loxostege sticticalis*) in North America. It attacks the host when the latter has completed the construction of its cocoon but before pupation occurs. In the field, the parasite is particularly in evidence at the end of the second generation of webworm on the beet crop, attacking the overwintering larvae during the mild, sunny weather of the Fall months. The parasite larva leads an ectoparasitic existence, the host being paralysed by the parent female parasite before the egg is laid. The fully-grown parasite larva spins a cocoon within that of the host which it has destroyed. Only one parasite individual can develop to maturity on each host individual.

Material for shipments to South Africa was reared in the laboratory using hibernating larvae of *L. sticticalis* in their cocoons. This host supply was obtained by large-scale field collections made during the Fall in the beet-growing

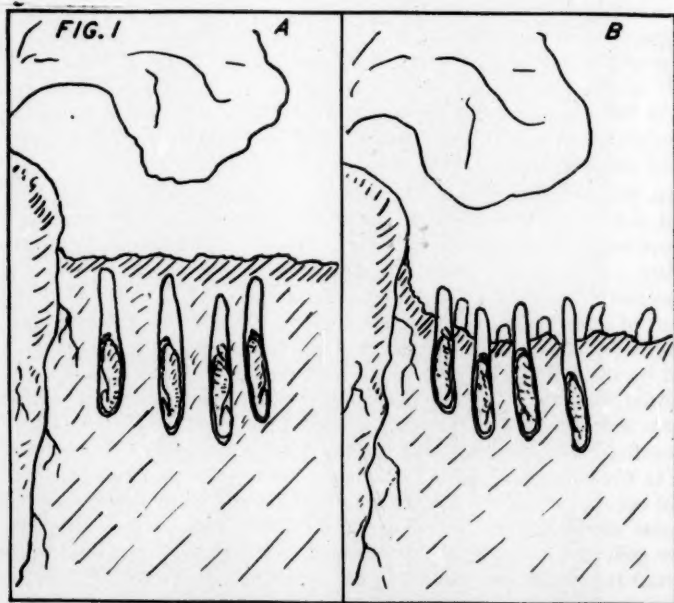


FIG. 1. Diagrammatic representation of cocoons of *Loxostege* in the soil: A.—when first formed; B.—exposed by removal of surface soil by wind or rain.

areas of southern Alberta. Parasite females readily attacked these larvae when the cocoons containing them were exposed in cages kept in bright daylight.

The host/parasite relationships are typically those of Group II, the host being in a position where it is afforded some protection and concealment from the parasites. The host is still in an active stage but its activity is considerably reduced and is restricted by the presence of the enveloping cocoon which also serves to prevent its escape from the parasite once the cocoon has been located. In Nature, the cocoon is further covered by a thin layer of soil, being constructed by the mature larva just beneath the surface of the ground. The cocoons are arranged with the long axis vertical in the soil, the upper end being just below the soil and the lower end occupied by the larva (fig. 1).

This, however, constitutes only a very flimsy barrier and it is often removed entirely or in part by the washing action of rain or by the high winds which frequently sweep over the open prairie, so that the upper ends of the cocoons are often left exposed above the soil surface (fig. 1B). The examination of the host by the ovipositing female is limited by this factor and recognition of the actual host (the larva) as a suitable one for the reception of progeny is presumably dependent upon the exploratory function of the tip of the ovipositor, either wholly or partially. Superparasitism commonly occurs in the laboratory under certain conditions, more especially when the ratio of hosts to parasites is small.

In the experiments about to be described, mated females of *Cryptus* of the same age were fed during the pre-oviposition period lasting a few days and were then placed singly or in definite numbers in small cages for testing. The cages used were $3\frac{1}{4}$ inches wide by $2\frac{1}{2}$ inches deep by $3\frac{1}{4}$ inches high (inside measurements). The top, bottom and sides were of wood, the back of muslin and the front, which acted as a sliding door, of thick celluloid. A hole, $1\frac{1}{2}$ inches in diameter, was bored through each side and was covered with muslin to provide an adequate through ventilation. Females in each cage were provided with water, sugar and split raisins. Host cocoons were scattered at random over the floor of the cage and left for the duration of the experiment. The experimental series were all kept in daylight at a constant temperature of 75°F . and with a relative humidity of 65 percent, both of which were obtained in an air-conditioned room.

In the technique outlined here, the position differs from the normal field conditions in that the host cocoons are wholly and freely exposed and are not partially protected by a layer of soil. Also they are lying horizontally instead of being supported vertically as they occur in the soil (fig. 1). Thus, the whole of the cocoon can be explored by the parasite instead of only one end as in the field. This, however, does not materially alter the general host/parasite relationship. In the field, the parasite is presumably able to accomplish just as efficient an exploration of the suitability of the host larva within the cocoon since the ovipositor is adapted to this purpose in its length. On the other hand, host finding may possibly be rendered more simple by the laboratory method since a greater area of each cocoon is exposed in relation to the total surface area occupied by the host population.

The texture of the earthy outer covering of the cocoon has an important bearing upon parasitism by *Cryptus*. In comparative tests it was found that cocoons which had been formed in sandy soil were much more readily accepted than were those constructed in a heavy clay soil. The latter were tough, especially when slightly damp, and the parasite female experienced considerable difficulty in piercing the envelope with the ovipositor. A much higher parasitism occurred in cocoons from sandy soil, these being more easily attacked. It was

therefore necessary to use host material which had been spun up in the same kind of soil in order to obtain uniform results which could be used for comparisons. In the present instance, cocoons from sandy soil were used.

The above factor is no doubt of importance in determining the degree of control exerted over the host by *Cryptus* in the field. In clay formations the surface hardens after wetting and is less liable to become removed by wind or light rains than is a sandy coverage. In the former, therefore, cocoons are less likely to become exposed and are hence presumably harder for the parasite to find. Apart from the difficulty of penetration through the cocoon, the increased difficulty of searching for hosts is therefore likely to result in a lower proportion of the host population being attacked on heavy than on light soils. This is supported by field observations, since collections made on the former type of soil gave a much lower percentage parasitism than did those on sandy areas.

The Effect of Host Density

Series of from two to twenty-five hosts per unit area were used in the tests. Hosts were scattered at random over the floor of each of the small cages and a single mated female, ready for oviposition, was introduced into each cage and allowed to remain with the hosts for a period of 24 hours. All females used in the tests were of the same age and had received identical pre-oviposition treatment. At the end of the period, the hosts were removed and the cocoons opened up, parasitism and distribution of eggs of *Cryptus* among the host individuals being recorded before hatching occurred. There were six replications of each treatment, the means of which were tested and found to be statistically satisfactory.

(a) Effect on host utilization

With increasing host density through the series, the total number of hosts found and attacked (i.e., paralysed) by the female parasite during the 24-hour period also increased, although the *proportion* of the host population thus affected decreased. The increase in hosts attacked is shown in figure 2, while the percentage of the available population thus represented is illustrated in figure 3(A). The results obtained are in general agreement with the findings in experiments with *Chelonus* (Ulyett, 1949) and other parasites. It would appear that, as in the case of both *Chelonus* and *Microbracon*, the total number of hosts found by the parasite female is limited by the time which is available for searching the given area and also by the actual number of hosts present within the area. Success in *finding* of hosts is therefore a function of time and host density, being directly proportional to both.

In the case of *Chelonus*, it was not possible to distinguish between productive and unproductive attacks on host individuals, since only the presence of a parasite egg within that of the host insect gave any indication that the latter had been found and attacked by the parasite. It is therefore not known whether unproductive attacks do take place in the case of *Chelonus* and similar parasites or, if they do, what relation they bear to the number of hosts used for oviposition. It seems unlikely, however, that abortive attacks occur in this species. On the other hand, the nature of the host/parasite relationship in the case of parasites like *Cryptus* makes it possible to distinguish hosts which have been *attacked* only and those which have, in addition, been *used* for the purpose of egg-laying.

Not all of the hosts found and attacked by the parasite are used for oviposition. A varying proportion of the available host population is found to be paralysed but without parasite eggs. The proportion of hosts which is used by the female shows a progressive decline as the number of available hosts per unit area increases. This is at first rather abrupt and then becomes more gradual as is shown in the curve (fig. 3B).

A comparison between the curves for the proportion of hosts attacked and of hosts used (fig. 3) shows that, apart from the fact that the latter is much lower throughout than the former, the proportion existing between them is a fluctuating relationship which varies with the original host concentration per unit area. This relationship exhibits three main phases as the host density increases:

(1) at the lowest host density the number of hosts used nearly approximates to the number attacked;

(2) this is followed by a marked divergence between the curves which covers the next three points, i.e., over what may be called the intermediate host concentrations;

(3) at the higher host densities there is a gradual and perceptible increase in the proportion of the attacked hosts which is used for oviposition and the two curves approach one another again with increasing numbers of available hosts.

The underlying cause of this phenomenon is not explained by the experimental data available and any attempt to offer an explanation must be purely speculative at this stage. It is noteworthy that a similar relationship occurs in the case of the Braconid, *Microbracon hebetor*, which has oviposition habits closely resembling those of *Cryptus* as far as treatment of the host is concerned (Ullyett, 1945).

In the case of *Microbracon*, the host larva is paralysed within the restricted area which it normally occupies and usually more hosts are attacked than are used within the 24-hour period. The search for hosts was shown to take place in two distinct phases, namely, (1) a preliminary period during which the environment was searched for living hosts and during which all those found were presumably immobilized immediately by the female parasite; during this period no eggs were laid and the female fed on one or more of the paralysed hosts: (2) a second search, no doubt modified by previous experience gained during the preliminary search, which had for its object the re-location of the immobilized hosts; during this period oviposition on paralysed hosts took place. The indications were that the female *Microbracon* attempted to cover the given area thoroughly and first to immobilize all the hosts occurring therein before ovipositing. The advantages of this procedure in the case of a parasite whose progeny lead an ectoparasitic, and therefore a somewhat exposed, existence, are obvious.

It would seem, from the similarity between the results obtained in the two cases, that the female *Cryptus* follows a very similar programme. This is also strongly indicated by a test which was made and in which the length of time during which the host population was exposed to parasitism was increased. Two series of 2 females with 20 hosts in equivalent unit areas were subjected to 24 and 48 hour exposure periods respectively. There were eight replications of this comparison. The results are shown in Table I.

It will be seen that the number of hosts attacked during the two periods did not differ greatly but that the number used was more than twice as great over the 48-hour period as over 24 hours. Similarly, the total number of eggs deposited during 48 hours was more than twice the number laid during 24 hours. The increase in time therefore did not appreciably increase the number of hosts found and attacked by the parasite but it had the effect of more than doubling the proportion of attacked hosts which were actually used for oviposition. This suggests that the great majority of hosts attacked were found and paralysed during a search of the environment which occurred during a certain period on the first day and that subsequent operations were mainly confined to re-locating the already paralysed individuals with the object of depositing eggs thereon. The position is therefore much as was found with *Microbracon*, i.e., that the

TABLE I.

Cryptus inornatus: EFFECT OF LENGTH OF EXPOSURE ON HOST UTILISATION AND DISTRIBUTION OF PROGENY: 2 PARASITE FEMALES AND 20 HOSTS PER UNIT AREA.

	SERIES	
	A	B
Exposure time in hours.....	24	48
Hosts: attacked.....	8.4	11.0
used.....	3.1	7.5
= percent of available.....	15.5	37.5
Eggs: total number laid.....	4.1	9.3
per female.....	2.1	4.6
per host used.....	1.3	1.2
percent effective.....	75.6	80.6

finding and utilisation of hosts are two separate phases in the host/parasite relationship.

In the case of both *Cryptus* and *Microbracon* the indications are that some factor serves to limit the period over which the first of these phases takes place. Although many more hosts may still remain unattacked in the environment at the end of the 48-hour period, the parasite is apparently content to ignore these. It would appear that, at some point in the chain of events, the general search of the environment is discontinued and the parasite turns its attention to re-finding the hosts which it has already paralysed and to oviposition. This is clearly indicated in the comparative experiment just described and is also reflected in the curves of figure 3.

The actions of the female *Cryptus* during the periods represented in Table I may be roughly followed by means of an analysis of the events indicated by the data in the two series taken consecutively. Series A gives the results achieved during the first day's activities. At the commencement of this period, the two females between them paralyse a total of 8 hosts, or 4 hosts each. This number is approximately equivalent to the number of mature or nearly-mature eggs which are present in the ovaries at this time, as determined by dissection of females which were reproductively mature (see below). Of these eggs, each female lays two, using an average of one and one-half hosts in doing so. She retains two nearly-mature eggs in the ovaries and leaves two and one-half hosts which have been attacked but not used. This is the position at the end of the first day.

Series B shows that, during the second day, each female lays an average of 2.5 eggs which, theoretically, should take care of the attacked hosts left over from the previous day. The remainder of the time would then be spent in finding and attacking new hosts and we find that this is apparently the case, since each female finds a further 2 hosts during the period and uses them for oviposition. If the distribution of eggs were perfectly adjusted, this would leave no hosts remaining unused at the end of the second day. We could then draw up a balance sheet showing this relationship of eggs and hosts. Assuming that 4 eggs mature in the ovaries each day, this would be as follows:

DAY	SOURCE	EGGS			HOSTS		
		Mature	Laid	Left	Attacked	Used	Left
1	1st. day	4	2	2	4	2	2
2	1st. day	2	2	0	2	2	0
	2nd. day	4	2	2	2	2	0

At the end of the second day, two eggs are left over which will be used during the third day. The account is therefore kept balanced day by day with some eggs which are nearly mature always in hand. In this statement we have ignored fractions and have arrived at a balanced account on the assumption that the distribution of eggs is 100 percent efficient.

But the distribution of eggs by *Cryptus* is not a perfectly adjusted phenomenon, and although the underlying scheme is clearly a balanced one as far as attack and utilisation of hosts is concerned, we find that it becomes modified in practice so that the total number of hosts attacked is never wholly used for the purpose of oviposition. Some always remain unused and some hosts receive more than one parasite egg. This is a resultant of the fact that, during the first day, when more time is absorbed by finding and attacking the requisite number of host individuals, the parasite female is only 75 percent efficient in the distribution of her eggs; while over the whole 48-hour period she is only 80 percent efficient. Because of this, our balance sheet does not reflect the actual situation and we find that, contrary to expectation, some hosts are left unused at the end of the second day and that no eggs are available to take care of them.

It is evident that a number of factors contribute to the modification of the behaviour of the parasite during this phase of its life and that the resulting complex situation would be difficult to analyse experimentally. It will be more convenient to defer further discussion of host finding and utilization until the general behaviour of the parasite in the distribution of its progeny can be viewed as a whole.

(b) Effect on distribution of progeny

There is no significant correlation between the host density per unit area and the total number of eggs produced by the female *Cryptus* during the 24-hour period. Dissections of reproductively-mature females have indicated that a certain restricted number of eggs reach maturity or near-maturity within a given time and that this number is in the neighbourhood of 4 within the 24 hours under the conditions of the experiments. Provided that some hosts are available and are found during this period, the whole quota of mature eggs is deposited (usually 2 per day), irrespective of the actual number of hosts present. There is apparently no inhibition of the act of oviposition due to a scarcity of hosts; or the physiological necessity of releasing ova on maturity is sufficiently strong to overcome any such inhibition. The number of eggs laid was therefore always approximately the same in all the experimental series and coincided with the number indicated in the ovarian examinations, namely, about 2 during the first day and 2 per day thereafter.

These results agree very closely in principle with those obtained in the case of *Microbracon*, although the latter species can produce many more progeny

within the same space of time. The same or a similar explanation will no doubt hold in both cases.

In sharp contrast with these, *Chelonus* showed a highly significant positive correlation between the number of hosts supplied and the total daily production of eggs ($r = +.9575$). In this case, where no prior preparation of the host individual (as by paralysis) is required, the parasite continues to oviposit in hosts as and when found throughout the period; and most of the time is presumably spent in moving from one part of the environment to another in the search for hosts. Eggs apparently mature and are passed into the oviduct almost continuously during this period, so that there is little or no delay in their deposition other than that caused by the scarcity of hosts and the consequent difficulty of locating them in the environment and the time necessarily taken up with feeding and the like. The density of the host population governs the ease with which hosts are found and hence the rate at which oviposition can proceed and the total number of eggs which can be disposed of within the given time.

The total daily egg production, and hence the increase in the parasite population per unit of time, is therefore limited in the case of *Cryptus* and *Microbracon* by the habits of the species and by their functional adaptations. At the same time, the apparent necessity for depositing the eggs as they mature leads to the incidence of superparasitism at the lower concentrations of hosts and serves to mask any evidence of the ability of the female parasite to gauge the suitability of the host individual for the reception of her progeny under such conditions. It should be noted here that the lowest host density used did not provide sufficient hosts for the reception of the daily egg production so that more than one egg had, of necessity, to be laid on each host.

In all the hymenopterous parasites so far studied, the presence of a discriminative faculty which enables the female to distinguish between suitable and unsuitable hosts has been demonstrated. The degree of development of this faculty varies with the species concerned and the exercise of the faculty, or the success which attends its use, becomes modified by a number of environmental

TABLE II.

Cryptus inornatus: FREQUENCY DISTRIBUTION OF PROGENY BY SINGLE FEMALES AT DIFFERENT HOST DENSITIES.

EGGS PER HOST ATTACKED	f = number of hosts in series					
	A (2)	B (5)	C (10)	D (15)	E (20)	F (25)
0	2	13	31	36	50	55
1	4	11	22	21	33	42
2	4	6	6	8	2	9
3	1	6	4	3	0	1
4	3	1	2	0	2	1
5	1	0	1	0	0	0
6	0	0	0	0	0	0
7	1	0	0	0	0	0
Total hosts:	16	37	66	68	87	108
Total eggs	39	45	59	46	45	67
Mean eggs per host:	2.44	1.22	0.89	0.68	0.52	0.62

conditions so that it is seldom wholly effective under normal conditions. The possession of such a faculty by *Cryptus* is clearly shown by its behaviour under conditions of increasing host density.

As stated previously, an individual host can afford sustenance to only one larva of *Cryptus*. The deposition of more than one parasite egg per host therefore results in true superparasitism and wastage of progeny since only one of these eggs will be effective. A measure of the efficiency of the female in the distribution of progeny is hence obtained by taking the percentage of the total daily production of eggs which is effective. When this is done for the series at different host densities, a highly significant positive correlation ($r = +.9537$) is obtained between host density and the proportion of effective eggs (fig. 4). The actual distribution of eggs among hosts attacked in the series is shown in the frequency distribution in Table II.

From the curve and from the table, it is evident that, throughout the series, *Cryptus* females show convincing evidence of a strong tendency to deposit only one egg in each host, i.e., to avoid superparasitism.

There is an unvarying mode of one egg per host throughout the series except for the very lowest host density used (2 hosts per unit area) where the mode lies at 1.5 eggs per host. This is where the number of hosts falls short of the minimum daily requirements of the parasite. The percentage of the total hosts attacked which falls within the modal group shows a definite increase as the host density is increased (fig. 5), with fewer and fewer hosts receiving the higher numbers of eggs. The percentage efficiency of the female in distributing her progeny to best advantage therefore becomes greater in direct proportion with the greater concentration of available hosts.

The exercise of the discriminative ability by the female and the consequent efficiency in the distribution of eggs, however, is not perfect. It would seem that the percentage efficiency of the female in this respect is limited by circumstances and the indications are that it attains an asymptotic maximum somewhere in the neighbourhood of 80 percent. This is reflected in the mean of the number of eggs deposited per host larva used through the series (fig. 6), which was always more than unity. The reason for this partial failure lies either in the imperfect development of the discriminative ability in this species or in an imperfect utilization of attacked hosts, i.e., in failure to locate these in the second phase of searching in spite of the fact that a sufficient number of immobilized hosts is available for the reception of eggs laid during this period without involving superparasitism.

From the experimental data it is not possible to say which of these explanations is the true one or if either of them can be accepted. There is a possibility that both factors may play a part, although it seems more than likely that the time/host-density relationship may be the main underlying cause of the imperfection. Added to this is the influence of the physiological state of the female on the act of oviposition. It is easy to see that, if the physiological necessity of releasing mature eggs is a rhythmical phenomenon, this will further limit the time which is available during each day for both searching for new hosts and dealing adequately with the ones found and paralyzed previously.

An examination of the test recorded in Table I, however, affords confirmatory evidence of the discriminative ability of the female. After 24 hours, 8.4 hosts are attacked and 3.1 are used. Hence, after this period there are only 16.9 hosts remaining unused, of which some are still unattacked and some have been paralyzed. This means that only 8.5 hosts still suitable for oviposition are available for each female on the second day instead of 10 as at the beginning. The

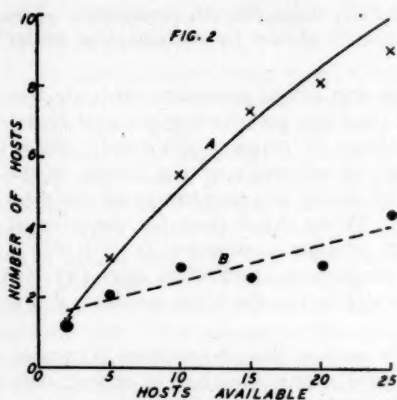


FIG. 2. *Cryptus inornatus*: A.—number of hosts attacked in relation to host density; B.—number of hosts used by the parasite for oviposition.

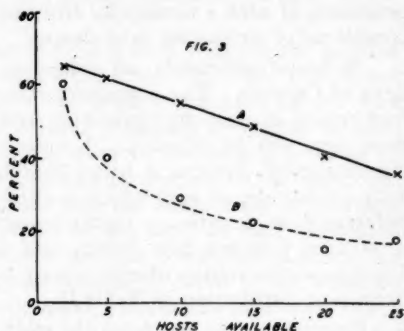


FIG. 3. *Cryptus inornatus*: A.—percentage of host population attacked; B.—percentage of host population used.

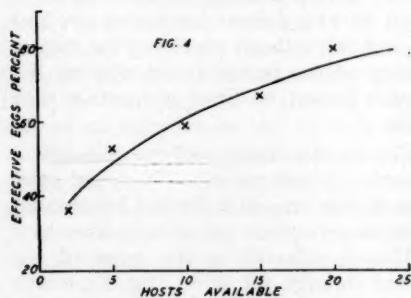


FIG. 4. Percentage of effective eggs laid by *Cryptus* females.

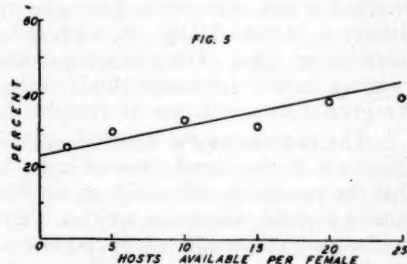


FIG. 5. Percentage of hosts falling in the modal group.

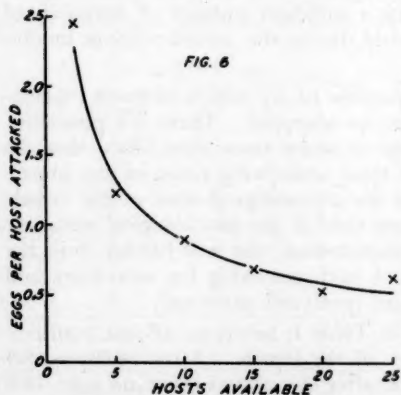


FIG. 6. *Cryptus inornatus*: Mean number of eggs per host larva.

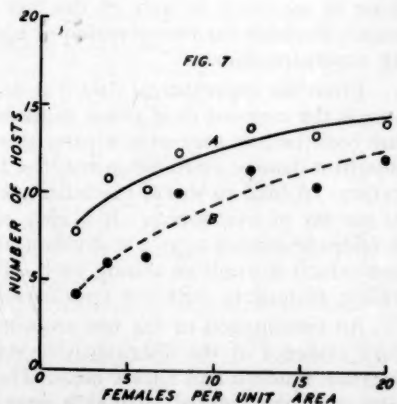


FIG. 7. *Cryptus inornatus*: A.—number of hosts attacked and, B.—number used when the parasite density is varied.

density of suitable hosts has been reduced yet, in spite of this, there is no significant difference in the efficiency of the female in the distribution of eggs. There is therefore evidence of an inherent discriminative faculty of a high order.

The Effect of Parasite Density

The previous experiments were made with single females per unit area. In Nature, however, the density of the parasite population within a given area will be a variable fluctuating from time to time and from place to place. A series of tests was therefore made in which the number of female parasites per unit area was varied while the number of hosts within the same area was maintained constant. The actual number of hosts supplied in each case was based upon the optimum number as observed in the previous experiments and was kept at 20 cocoons per cage. The number of females placed in each cage varied from 2 to 20. There were six replications of each series, the exposure time being 24 hours as before.

(a) Effect on host utilization

The relationship between the number of hosts found and the number used by the female parasites during 24 hours under different conditions of parasite density is shown in figure 7. The curves reflect the influence of the density factor on the activities of the population as a whole. It will be noted that, over the range of parasite concentrations used, the number of hosts found during the experimental period increased more or less gradually throughout (Curve A). The percentage of the available host population which was attacked also increased from approximately 38 percent at the lowest parasite density to a little over 70 percent at the highest concentration.

Similarly, the number of hosts used for oviposition by the parasite population increased as the latter increased (Curve B). The percentage of the available host population thus used rises from 21 percent to 61 percent through the series, while the percentage of the attacked hosts which is used for oviposition increases from 54 to 86 as the parasite density becomes greater.

The relationship in both instances is not a linear one and an inspection of the curves shows that the efficiency of the parasite population in finding and using hosts within the given time and under the conditions of the experiment, becomes progressively impaired as the density of parasites is increased. The series does not go far enough to show whether an asymptotic maximum is reached followed by a sudden decline such as was found in the case of *Chelonus*, but there is reason to believe that this would actually be found to occur at higher concentrations of parasites. The decided flattening of the curves at the higher densities point to this conclusion.

The number of hosts attacked by the individual females in the population shows a rapid decline as the number of parasites per unit area increases (fig. 8). Similarly, the number of hosts used per female decreases with increasing parasite density. The most rapid phase of this decrease occurs when the parasite density is lowest and is particularly marked where the latter is below about 6 females per unit area. After this, the decline is more gradual. The former phase takes place when there is still a relative abundance of hosts, or at least sufficient hosts for the daily needs of the parasite population and when the area available cannot be regarded as markedly overcrowded. Throughout the series, in fact, there are always some hosts which are left over (*vide* fig. 7) indicating that a shortage in the absolute number of hosts within the unit of area is not the limiting factor. This point will be discussed in more detail later.

It is interesting to note that, as the number of attacked hosts per female decreases, the number used for oviposition more and more nearly approximates

to the number attacked. This is readily understood when the daily physiological rhythm of egg-production by the parasite is taken into consideration and if the necessity for releasing the mature ova is conceded (*vide supra*). This explanation will be afforded support when the effect on oviposition is discussed.

It is evident that any sudden increase in the population of the parasite within a given area and with a given host population does not give a corresponding increase in parasitism of the host (and therefore in its control) which is commensurate with the sum of the *potential* capacities of the individual females. Some factor or factors step in to modify this capacity when more than one female is present in the area. One of these factors is undoubtedly the partly mechanical one produced by interference between the individual females during the search for hosts and oviposition. The parasites are robust, large insects and contacts between them almost invariably result in a degree of disturbance which not only interrupts the functional activity of the females concerned but helps to take up a certain proportion of the experimental period which might otherwise be more profitably employed. Observation of the parasite behaviour during this phase showed that it can be a very real factor in the modification of results. A second factor is the altered ratio between hosts and parasites which results from an increase in one of the populations in the unit area. This factor was shown to be of primary importance in the similar tests made with *Chelonus texanus*. This aspect will be dealt with below.

(b) *Effect on oviposition*

The total number of eggs laid by the parasite population as a whole during the 24-hour period increases in direct proportion to the density of that population and this it does in almost arithmetical progression. This is explained by the fact that the increasing parasite density has no significant effect upon the number of eggs laid by the individual females in the population (*vide* Table III). As stated

TABLE III.

Cryptus inornatus: EFFECT OF PARASITE DENSITY ON OVIPOSITION WITH HOST DENSITY CONSTANT PER UNIT AREA.

NO. OF FEMALES	TOTAL EGGS	EGGS PER FEMALE	EGGS PER HOST USED	EFFECTIVE EGGS PERCENT
2	6.00	3.00	1.43	69.5
4	9.33	2.33	1.56	64.3
6	12.83	2.14	2.03	49.3
8	22.17	2.77	2.18	45.9
12	28.00	2.33	2.43	41.1
16	25.83	1.61	2.46	40.7
20	41.50	2.08	3.41	29.3

above, the number of eggs maturing in the ovaries per unit of time is a constant and, provided some hosts are available, these eggs are released irrespective of the actual number of hosts which are found. Hence the production of eggs per female per day is unaffected and there is no significant difference between the different parasite density series in this respect. As a direct consequence, the discriminative faculty of the female parasite becomes obscured and superparasitism

supervenes. No matter what the parasite density may be, the total number of eggs deposited by the entire population within the given time is equivalent to the simple product of the number of individuals present and the number of mature eggs produced in the ovaries of individual females during that time. This contrasts strongly with the behaviour of *Chelonus* under similar conditions of varying parasite density where the number of eggs per female showed an inverse relationship to the population density.

The peculiarity exhibited by *Cryptus* thus makes an increasing population of potential progeny available with an increase in the number of parasites per unit area, since a fixed number of eggs are added with each individual female per unit of time and all of these eggs are automatically released irrespective of host density. A sudden increase in the host population can therefore be made use of by the parasite immediately. It is clear that the efficiency with which these eggs will be distributed and therefore the effect on the future parasite population, will depend mainly upon the number of hosts available within the given universe.

TABLE IV.

Cryptus inornatus: DISTRIBUTION OF PROGENY AT VARYING PARASITE DENSITIES: FREQUENCY DISTRIBUTION OF EGGS IN HOSTS.

EGGS PER HOST ATTACKED	F = NUMBER OF HOSTS IN SERIES						
	A (2)	B (4)	C (6)	D (8)	E (12)	F (16)	G (20)
1	20	21	20	32	32	21	25
2	6	12	12	10	11	18	10
3	1	2	4	7	12	15	8
4	.	0	2	4	6	2	6
5	.	1	0	5	5	2	9
6	.	.	1	2	2	3	5
7	.	.	0	1	1	1	6
8	.	.	0	.	0	0	1
9	.	.	1	.	0	0	1
10	1	1	0
11	2
TOTAL HOSTS:	27	36	40	61	70	63	73
TOTAL EGGS:	35	56	79	133	168	155	249
MEAN EGGS PER HOST:	1.3	1.5	1.9	2.2	2.4	2.5	3.4

(c) *Effect on distribution of eggs*

The frequency distribution given in Table IV shows the grouping of hosts in each series according to the number of parasite eggs found on them after 24 hours' exposure to various parasite densities. The records are for attacked hosts only. In this grouping, the discriminative ability of the female parasite in choosing suitable hosts is again strongly evident and there is a definite tendency to avoid depositing more than one egg in each host attacked. The mode is expressed by the group having only one egg per host in all the series. It is also evident, however, that an increasing number of parasite females per unit area has the effect of progressively impairing this capacity when the host population remains constant. At the lowest parasite density, 74 per cent of the hosts had only one egg. At the highest concentration of parasites only 34 percent of hosts fall into this group and an appreciable number of hosts bear 5 or more parasite

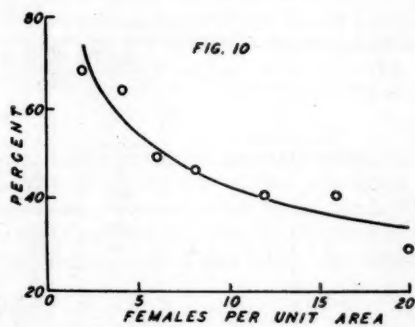
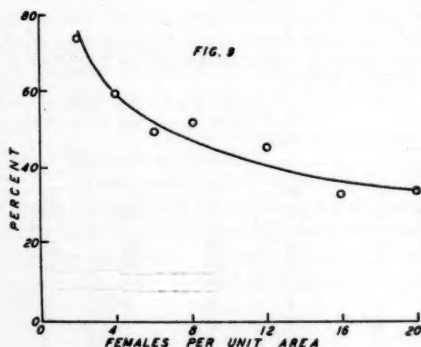
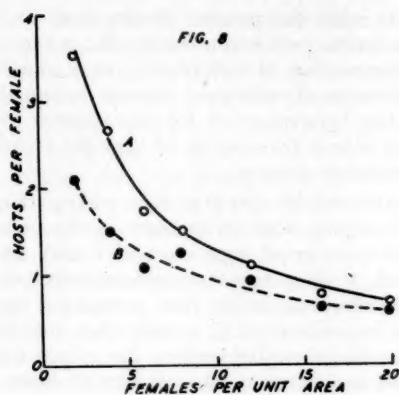


FIG. 8. *Cryptus inornatus*: Varied parasite density and A.—number of hosts attacked per female; B.—number used per female.

FIG. 9. Percentage of hosts falling in the modal group when parasite density is varied.

FIG. 10. *Cryptus inornatus*: percentage of effective eggs per female when the parasite density is varied.

eggs each. The regression of the percentages of hosts falling within the modal group on the parasite density is a curvilinear one (fig. 9).

Since only one parasite larva can develop to maturity on each host individual, this decrease in the percentage of the host population which receives only one egg will result in a corresponding decrease in the efficiency of the female parasite in distributing her progeny to the best advantage. This will be further aggravated by the fact that the number of hosts attacked per female decreases with increasing parasite density in a like manner while the total number of eggs produced per female remains constant. Thus we find that there is a marked decrease in the percentage of the daily eggs which are effective, i.e., there is an increase in the number of eggs which are laid on each host attacked and therefore in the number which are wasted. This is significantly correlated with the increase in parasite density (fig. 10).

It is necessary to draw attention to the fact that, while increasing parasite density, itself, is a factor of importance which influences the relationship between host and parasite and modifies the potentialities of the latter in the distribution of its progeny, under the conditions of the experiment it is not the sole factor

operating to this end. Since the absolute number of hosts per unit area was maintained constant over all the series, it follows that the ratio of hosts to parasites enters the picture as a significant variable in addition. Because of this, the efficiency of the parasite at the higher population densities will be influenced not only by the effect of the parasite density itself but also by an actual shortage of hosts.

In consequence of this, there will be insufficient hosts to ensure the optimum condition of one parasite progeny per host since, where 20 *Cryptus* females are present, there is, at the most, only one host per female which is available within the universe. Since each female must release approximately 2 eggs during the period given, it is obvious that a considerable proportion of the host population which is found and attacked must receive more than one egg per individual and that some hosts will receive several eggs. This is shown by the results in series G. Nevertheless, the modal group here remains the same as in all the other series and the fact that 34 percent of the hosts attacked still fall into this group in spite of considerably adverse conditions, shows that the discriminative faculty possessed by *Cryptus* females is a powerful factor in the behaviour of the parasite and in the survival of its population. The significance of the host/parasite ratio in relation to distribution will be considered more fully.

(CONTINUED NEXT ISSUE)

The Role of Morphology in Systematics¹

By W. J. BROWN

Ottawa, Ont.

The following notes consider very briefly a very large field. They apply primarily to zoological systematics. They reflect my respect for the thoughtful field naturalist and, probably, some other prejudices. They reflect my interest in the species rather than in the higher categories, and are of course influenced by the limitations of my experience.

Everyone who has studied biology appreciates the classic role that comparative morphology has played in the development of systematic biology. Since the earliest times, man has recognized the empirical fact that animals and plants can be sorted, with greater or less difficulty, into groups that can be called kinds or species as well as into higher groups. One of the important features of the system devised by Linnaeus is the concise morphological definition of the species and of the higher groups. Linnaeus and the other eighteenth-century systematists, as best they could, recorded distributions and food-plants, showing that they appreciated some non-morphological attributes of species. However, as they received more and more material from foreign lands, they became more and more dependent on morphology as a basis for their systematics, for they usually knew nothing of their foreign specimens other than country of origin. In those pre-Darwinian days, the principles of special creation and the immutability of the species were accepted generally, and the morphological method seemed adequate; the systematist therefore considered that his work was well founded philosophically and that his method was obvious. Such was the position of systematics and the role of morphology in systematics when Darwin's *Origin of Species* was published in 1859.

¹Contribution No. 2640, Division of Entomology, Science Service, Department of Agriculture, Ottawa, Canada. Read as part of a symposium on systematics at the eighty-sixth annual meeting of the Entomological Society of Ontario, Winnipeg, November 4, 1949.

The impact of Darwinism on systematics was very great. The theory of common descent implied that species and higher groups were continuous with one another, morphologically and physiologically. Darwin himself pointed out how vague the boundaries between species and varieties really were in the minds of systematists and how difficult it was to define the term species. He considered that the term, species, was given arbitrarily and for convenience to a number of individuals which resembled (i.e., morphologically) one another closely, and that the species and the variety were not essentially different. Thus, for many biologists, the species became a thing that existed only in the mind of the systematist, and systematics became a pseudoscience. Systematics became the step-child of biology, especially in Europe, where universities relegated the subject to the museum worker, who was limited to a morphological approach, and to the amateur, who was usually untrained in scientific method. Only the thoughtful field naturalist continued to believe that the species had any reality in nature and a greater degree of objectivity than had the higher taxonomic categories. Systematics had lost its old philosophical foundations without gaining new ones and, in practice, remained pre-Darwinian. Writing of invertebrates in 1877, Huxley⁴ stated: "The things classified are arranged according to the totality of their morphological resemblances, and the features which are taken as the marks of groups are those which have been ascertained by observation to be the indicators of many likenesses or unlikenesses." Thorpe⁷, in 1931, defined the species "as a group of individuals distinguished from all other groups by the common possession of certain structural characters"; he added that biological races exist when "the individuals of a species can be divided into groups, occurring in the same locality and showing definite differences in biology, but with structural differences, either very slight and inconstant, or completely absent." These statements, and a great many others which could be cited, show how the morphological concept of the species persisted, and how the species concept of many biologists remained arbitrary until almost the present time. Systematists who were not satisfied with a morphological or subjective concept of the species remained in a very unsatisfactory position. Ferris⁸ wrote in 1928: "And so out of it all we are still left with no actual definition of a species. It remains still a matter of point of view and of opinion." The position of systematics at that time was most unfortunate.

A change in this position had its beginnings about 1924. It was discovered that populations in nature possess reserves of hereditary variability, a considerable part of which is hidden in the populations in a heterozygous state. Certain geneticists began to study this variability, and the science of population genetics was born. Progress was very rapid, and in 1937 Dobzhansky² published his *Genetics and the Origin of Species*. This organized the scattered work in population genetics and made it available generally. The geneticists and others, following studies on variation in natural populations, on selection, on isolating mechanisms, and on species as natural units, adopted and restated a species definition of the field naturalists, and this definition is becoming generally accepted. To many biologists, systematics appears to be well founded and prepared to take its proper place in biology for the first time since the *Origin of Species*. In 1948, Mayr⁶ wrote that the recent changes in systematics can be grouped under three headings. (A) There has developed a new species concept, that of the geographically variable or polytypic species, and a trinomial system of nomenclature has been adopted to cover it. (B) The population is the basic unit in taxonomy. No specimen can be considered 'typical'; what are 'typical' are the statistical constants of the population to which a given individual belongs.

(C) The morphological definition of the species, which emphasizes degree of morphological difference, is replaced with a biological definition which emphasizes rather the completeness of the gap between species. These viewpoints, especially the second and the last, changed greatly the role of morphology in systematics as it was commonly practiced. Mayr added that most animal systematists consider the following seven statements as well substantiated. (1) Animal species have reality in nature and are well defined (but not necessarily by morphological characters) except in borderline cases. (2) The term species should be defined on a biological (not a morphological) basis, with reproductive isolation as the criterion. Thus, *a species is a group of actually or potentially interbreeding natural populations that is reproductively isolated from other such groups*. (3) Species are often composed of populations which are sufficiently distinct to be recognized (in nomenclature) as subspecies or geographical races. (4) The genetic differences that exist between the geographical races of a species may affect ecological preferences as well as morphological and physiological characters; in fact, all characters of species are subject to geographical variation. (5) When portions of a species are subject to geographical or spatial isolation, the portions tend to drift apart genetically at variable rates. (6) When isolation is sufficiently long and sufficiently complete, there develop isolating mechanisms which will inhibit the interbreeding of the two daughter species after the elimination of the extrinsic isolating factor. (7) Except in borderline cases, there is a 'bridge-less gap' (reproductive isolation) maintained by isolating mechanisms between species that co-exist at the same locality. Mayr could have added other statements, including the following. (1) The characters, morphological and otherwise, that differentiate species and subspecies are of the same order. (2) Genera and higher categories, unlike the species, have no reality in nature, in that their limits are subjective.

The acceptance of these ideas is modifying the attitude and method of the working systematist largely because the ideas modify the role of morphology in systematics. The systematist, believing that species have reality in nature, seeks to identify his species with nature and not subjectively with specimens or published descriptions. Believing his species are physiological (in the broadest sense) entities rather than morphological entities, he considers morphological knowledge alone superficial. Labels bearing ecological data are important to him, and, because of dates, localities, or food-plants given on such labels, he may question the identity of specimens which are morphologically identical. He will recognize species that cannot be segregated by morphological characters, and he will go to the field to study the taxonomy of such species. In fact, the field will sometimes be more important to him than the museum or the laboratory in his study of the attributes of races and species. He does not neglect the morphological attributes of his species, but he compares population samples rather than individual specimens, and his collection becomes a collection of such samples. As he does not expect samples from different localities to agree always in their morphological characters, he is bedevilled by problems of evaluation. Do the morphological differences between two populations from different regions indicate two species or two geographical races of one species? Such questions can no longer be answered arbitrarily, and knowledge other than the morphological is usually lacking. Considering the subspecies (geographical races) recognizable by morphological characters, do all of them or only the most strongly characterized merit names? If only the latter do, where is the line to be drawn? And what is to be done, nomenclatorially, with subspecies that differ

only physiologically? In such a manner does the working systematist subordinate morphology today.

Why was it that, during almost half the period between the publication of the tenth edition of *Systema Naturae* and the present day, systematic biology occupied such an unsatisfactory position? In my opinion, it was due almost entirely to the role that most biologists gave to morphology in systematics. The morphological approach to systematics was overemphasized, so that, in the minds of many biologists, systematics was based exclusively on morphology, as is shown by the purely morphological definitions of the species that were so widely accepted. However, biologists rarely agree perfectly, and during the post-Darwinian period many systematists, to the extent that they were field naturalists, believed in the reality of species, although they were usually unable to defend satisfactorily their belief. That an arbitrary, purely morphological concept of the species was unnecessary even in early post-Darwinian times is shown by the writings of a few. For example, Walsh³, who was greatly impressed by the *Origin of Species*, discussed the nature of species in a paper published in 1864. In this paper, Walsh seems at times to overemphasize the role of morphology. However, he wrote: "The only valid practical criterion of specific distinctness is the general non-existence, either actually ascertained or analogically inferred, of intermediate grades in the distinctive characters, whence we may reasonably conclude that the two supposed species are distinct, i.e., that they do not now in general mix sexually together, or if geographically separated, that they would not do so, supposing them to be placed in juxtaposition . . . it is immaterial whether the distinctive characters be slight or strong . . ." He continued: "I consider as species all forms which do not habitually intermix in a state of nature. . . . Others require in addition, that the distinctive characters should be of a certain type, which is left to be fixed and defined in each particular genus by certain varying and somewhat indefinite rules." These statements are a rejection of morphological and arbitrary concepts of the species and acceptance of reproductive isolation as the criterion of specific distinctness in the manner of the present-day systematist. Also they affirm the reality of the species in nature. Walsh wrote, "Species often run into what are known as geographical races, when separated into two or more distinct groups by physical barriers." This is the present-day concept of the geographically variable or polytypic species. We have noted Mayr's three developments that are responsible for the change to present-day systematics, also his seven statements which incorporate some of the views now widely held among animal systematists. The subject of Walsh's paper was not geographical variation, and Walsh's theory of the evolution of isolating mechanisms was, not surprisingly, hopelessly Lamarckian. But he implied strongly or stated specifically his acceptance of all of Mayr's three developments and five of Mayr's seven statements. Except for his Lamarckianism, Walsh's views were essentially those of the present-day systematist. There is abundant evidence in the literature that many systematists, of both pre- and post-Darwinian times, did not limit themselves to a purely morphological approach to their subject. During the last decade, some authors have used the term "new systematics" to distinguish the systematic thought of recent years from that of earlier periods. But it should be remembered that most of the fundamental ideas of the present day are not new.

The place of morphology in systematics, abused and misunderstood in the past, is being re-evaluated generally and is secure because of the empirical fact that the majority of animals can be sorted into the groups that we call species. And without an appreciation of morphological relationships, one cannot easily

and quickly deduce knowledge of a strange species to the benefit of a practical problem. The working systematist is always aware that he is overlooking morphological characters, because of the limitations of his equipment and methods. And so, considering the species to be real and discrete, he may wonder whether the pre-Darwinian systematist was not right after all in believing that all species differ morphologically from one another.

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Orygma luctuosa in North America (Diptera, Coelopidae)

By CURTIS W. SABROSKY

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On August 28, 1949, over beach drift and seaweed at Matane on the Gaspé Peninsula, Quebec, the writer collected a series of flies presumed to be *Coelopa frigida* (F.). Later examination revealed the capture of two males of *Orygma luctuosa* Meigen, a peculiar coelopid fly with small eyes, extremely broad cheeks, and broad, flat facial carina. Inasmuch as this European species had apparently been recorded only once before from North America, it seemed desirable to place the find on record.

While preparing the note, the writer chanced upon the published figures of *Eugenacephala salsa* Johnson, said to be a species of Scopeumatidae (Scatophagidae), and he recognized at once that it must be *Orygma*. Through the courtesy of Dr. J. Bequaert of the Museum of Comparative Zoology, male and female paratypes of *E. salsa* were borrowed for study, and the suspected synonymy was confirmed. It then appeared probable, from discrepancies between Johnson's description and specimens, that *E. ruficeps* Curran (1925) was also a synonym, for the middle femora in *salsa* actually lack bristles, though Johnson wrote "All of the femora with prominent rows of flexor and extensor bristles." This synonymy has been confirmed through the kindness of Mr. Guy Shewell, who compared a specimen with the type of *E. ruficeps* Curran in the Canadian National Collection. Mr. Shewell also reports that collection to contain a number of specimens (as *salsa*) collected by W. J. Brown from localities on the St. Lawrence Gulf.

The synonymy and North American records may be summarized as follows:

Orygma Meigen

Meigen, 1830, Syst. Besch. VI: 6. Type, *O. luctuosa* Meigen (Monotypy).
Eugenacephala Johnson, 1922, Occ. Papers, Boston Soc. Nat. Hist., 5:22.

Type, *E. salsa* Johnson (Orig. desig. and monotypy). (NEW SYNONYMY).

***Orygma luctuosa* Meigen**

Meigen, 1830, Syst. Besch. VI: 6, pl. 55, figs. 13-17 (Europe).

Eugenacephala salsa Johnson, l.c., p. 22, figs. 3, 4 (Mass., Maine, N.H.); Johnson, 1925, *ibid.*, 7:243; Johnson, 1927, Biol. Survey Mt. Desert Region, Pt. I, p. 213; Procter, 1946, Biol. Survey Mt. Desert Region, Pt. VII, p. 414. (NEW SYNONYMY).

Eugenacephala ruficeps Curran, 1925, Canad. Ent. 57:25 (Labrador); Johnson, 1929, Psyche 36:145. (NEW SYNONYMY).

Eugenacephala ruficeps Johns. [sic]; Procter, 1938, Biol. Survey Mt. Desert Region, Pt. VI, p. 358, and 1946, Pt. VII, p. 414 (Mt. Desert I., Maine).

Orygma luctuosa Meigen; Procter, 1938, Biol. Survey Mt. Desert Region, Pt. VI, p. 357 (S.W. Harbor, Mt. Desert I., Maine, bred from seaweed, said to be first American record); Procter, 1946, *ibid.*, Pt. VII, p. 413 (record repeated).

Because of several long, black, bristlelike hairs among the fine hairs bordering the posterior spiracle, *Orygma* may be traced in some keys to the family Sepsidae, which it resembles also in the abruptly abbreviated anal vein and broad, flat, facial carina. In this last respect, and in habitus, *Orygma* also seems close to *Omomyia* Coq., a genus which has been variously placed in Scopeumatidae, Coelopidae, and Pallopteridae.

Obituary

We regret to announce the death of two members of long standing in the Entomological Society of Ontario.

Mr. Victor Kitto, formerly a member of the Department of Health, died on December 10, 1949. He was a student of the Coleoptera and a member of the Society from 1913.

Mr. A. D. Hall, of Great Village, Nova Scotia, died on December 31, 1949. Mr. Hall who was born in Birmingham, England, and was a watchmaker by trade, was an enthusiastic amateur entomologist and had been a member of the Entomological Society of Ontario for many years. He bequeathed his collection to the Agricultural College at Truro.

W. R. THOMPSON.

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